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# DECIPHERING LANDSCAPE MOSAICS OF NEOTROPICAL TREES: GIS AND SYSTEMATIC SAMPLING PROVIDE NEW VIEWS OF TROPICAL RAINFOREST DIVERSITY<sup>1</sup>

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## ABSTRACT

How are tree species within tropical rainforests distributed at the landscape scale? One research site, the La Selva Biological Station in Costa Rica, offers exceptional tools for addressing this question: a documented flora, soil and topographic maps, a reserve-wide grid, and a Geographical Information System (GIS). My colleagues and I have combined these tools with highly replicated systematic sampling over 600 ha of old growth to investigate patterns of forest composition within this lowland tropical wet forest. This approach has revealed features of within-forest heterogeneity that had remained "invisible" during extensive fieldwork by many researchers at La Selva. Examples are: a doubling in density of the guild of subcanopy and canopy palms between flat terrain and increasingly steep topography; strong shifts in density of many palm and tree species over La Selva's limited gradients of soils and topography; evidence of human harvesting of one palm species from old-growth forest; and evidence suggesting indigenous human activity deep within the reserve (the co-occurrence of a previously unrecognized zone of alluvial soil, buried charcoal, and an avocado tree). These studies have also added 15 tree species to the known flora of this intensively researched forest. Although La Selva's support for such landscape-scale studies is exceptional, even in remote tropical forests it is now possible to systematically sample and geo-reference information on site variation and species distributions using newly available Global Positioning Systems. Findings can then be cross-referenced with current and future site data, using a GIS. Although such efforts, especially the development of a GIS, require considerable investments of time and expertise, the payoff can be a more robust understanding of the distribution of tree diversity and species abundances over tropical rainforest landscapes.

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How many tree species exist in tropical rainforests? Where are they found, and how and why do their abundances vary spatially? Such information is critical for understanding the biodiversity, structure, and function of this biome and for conserving representative sites into the future. Unfortunately, these superficially simple and basic questions about the world's tropical rainforests are currently unanswerable.

One reason for this situation is extreme species richness. Those carrying out inventories of lowland forest in the wet Neotropics typically find 80–300+ species of trees  $\geq 10$  cm in diameter co-occurring in a single hectare (Valencia et al., 1994; Gentry, 1988; Foster & Hubbell, 1990; Lieberman et al., 1985a). In addition to the sheer numbers of taxa, identification is made challenging by the sterile condition of most trees at any given time. Many

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<sup>3</sup> This paper is dedicated to the memory of Alwyn H. Gentry (1945–1993), who made extraordinary contributions to the current understanding of the world's tropical forests.

tropical wet forest plants only fruit and flower episodically, some even supra-annually (cf. Newstrom et al., 1994; Appanah, 1990), and in addition any plot includes many immature stems. Even when reproductive specimens can be obtained, identifying tropical rainforest trees is often not straightforward. Reference collections, keys, and treatments are incomplete and constantly evolving, as are the accepted names for given taxa. Much of the tree diversity occurs in problematic families, such as Sapotaceae, Myrtaceae, and Lauraceae, with difficult-to-separate species. For these and many other groups, any hope of definitive identification often rests with a few contemporary specialists, who are usually halfway around the world from the study site. Finally, as Gentry (1994) and others have pointed out, whenever a great investment of time and personnel results in distinguishing all tree species in a tropical rainforest plot, some to many of these turn out to be new to science. The bottom line is that, for most tropical forests, the tree flora remains poorly known. Only a handful of tropical forests have been well studied floristically (e.g., sites in Gentry, 1990; Condit, 1995). Even in the exceptional sites with long histories of plant collecting and well developed floras, new species of trees keep turning up as researchers look carefully at the forest.

Deciphering the nature and determinants of tree distributions within the world's tropical rainforests is clearly going to be difficult, but not simply because of these issues of taxonomic complexity and incomplete collecting and monographing (Gentry, 1992). A second obstacle, a corollary to the richness of these tree communities, is the local rarity of most species. For example, in a Costa Rican lowland wet forest (La Selva), 81% of the tree species inventoried had densities of  $\leq 1$  individual  $\geq 10$  cm in diameter per ha (data from Lieberman et al., 1985b). The resulting sample-size limitations mandate innovative approaches for studying the distributions of most tree species within these forests.

A third challenge is presented by another kind of diversity, the abiotic heterogeneity of tropical forest landscapes. Those monotonous expanses of green viewed from overflying planes are actually complex mosaics of forest types. Underlying the species-rich tree communities are landscapes of interdigitated terrain types. The component patches differ among themselves in many ways: topography, soil nutrients, and hydrology (Ashton, 1964; Austin et al., 1972; Baillie et al., 1987; Kahn, 1987; Gentry & Ortiz S., 1993; Ruokolainen & Tuomisto, 1993; Tuomisto et al., 1995; Clark et al., 1995; Duivenvoorden, 1996), disturbance histories (e.g.,

very large blowdowns; Nelson et al., 1994), flooding regimes (Salo & Rasanen, 1989; Foster, 1990), and histories of human intervention (Gordon, 1982; Gómez-Pompa & Kaus, 1990; Anderson, 1990; Bush & Colinvaux, 1994). In tandem with the incomplete knowledge of floristics goes a poor understanding of this spatial heterogeneity in tropical rainforest landscapes. Part of this has simply been due to the difficult logistics and the size of the problem—for many areas of tropical rainforest, studies of all of the above factors are still lacking. Efforts to discern the spatial mosaics within these forests will greatly benefit from an interdisciplinary approach. Tropical forest ecologists and plant systematists, particularly those trained in North America, often have little training in soils and geomorphology. Soil scientists and geologists are well prepared to evaluate the spatial variation in these site factors, but usually lack any knowledge of plant systematics. Similarly, anthropologists, historical geographers, and archaeologists have special skills for assessing current and historical potential human impacts within a forest. Understanding the patterns and causes of tree distributions within tropical rainforests will require pooling information and insights from these disparate disciplines.

In this paper, I describe in-progress research at a rainforest site that offers an unparalleled set of tools for deciphering the spatial mosaics within the tree community. This work has built on three key elements: an extensive site database generated through decades of research in many disciplines; the use of highly replicated, systematic sampling to study the forest at the landscape scale; and synthetic analysis of complementary types of spatial information, made possible by a Geographical Information System (GIS). I show how this combined approach is revealing levels of spatial heterogeneity within this forest that were previously unrecognized, in spite of the extensive research history of the site. I review the process of developing these research tools and then assess the potential applicability of these and other promising new methods for extending such studies more generally in tropical rainforest.

#### AN EXCEPTIONAL SITE FOR ASSESSING RAINFOREST LANDSCAPES

This research was carried out at the La Selva Biological Station of the Organization for Tropical Studies (OTS), an international consortium of universities and research institutions. La Selva (Fig. 1) is a 1550-ha reserve located in the Caribbean lowlands of northeast Costa Rica, Central America

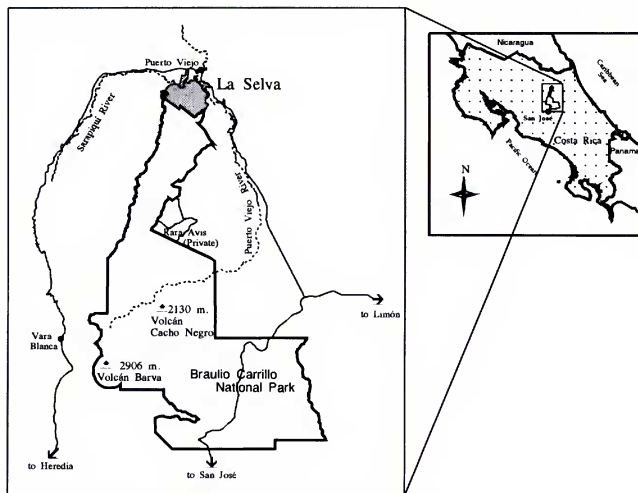


Figure 1. Location of the La Selva Biological Station, Costa Rica, Central America (map produced by J. Juárez, OTS).

( $10^{\circ}26'N$ ,  $84^{\circ}00'W$ ; elevation 37–150 m). It is contiguous with Braulio Carrillo National Park (47,000 ha), which protects a forested transect extending from the lowlands to 2900 m above sea level. La Selva is classified in the Holdridge Life Zone System as Tropical Wet Forest (Hartshorn & Hammel, 1994). Mean temperature is  $26^{\circ}C$ , and mean annual rainfall is 4 m, with every month averaging at least 100 mm of rain (Sanford et al., 1994). Detailed site information is given in McDade et al. (1994).

Due to a combination of factors, La Selva offers exceptional research support for landscape-scale studies in tropical rainforest (Clark, 1990). Over nearly 30 years, the station has evolved from a rustic farmhouse at the edge of a remote lowland forest into one of the most intensively studied tropical rainforests worldwide. Currently more than 250 researchers a year at La Selva carry out studies in the fields of systematics, evolutionary ecology, long-term population dynamics, conservation biology, soil science, forestry, ecosystem ecology, and atmospheric chemistry. This multifaceted research activity has built up a rich site database and creates opportunities for interdisciplinary studies. The station's research infrastructure includes four additional elements that have been critical for our

studies of the spatial heterogeneity of tree distributions: a documented flora, a reserve-wide grid system, a detailed soils map, and a site GIS.

#### PLANT IDENTIFICATION

For the non-specialist, identifying plants is easier at La Selva than at most tropical rainforest sites. The in-progress La Selva Flora Project (Wilbur, 1986) has produced a checklist of 1852 vascular plant species (R. Wilbur, pers. comm.), including 323 species of trees  $\geq 10$  cm in diameter (Hartshorn & Hammel, 1994). Several treatments have been published (see Hartshorn & Hammel, 1994), and the full flora is nearing completion. The station has a small reference herbarium, plus a collection of ca. 4000 plasticized high-contrast xeroxes (method developed by R. B. Foster) of La Selva specimens deposited at Duke University Herbarium, headquarters of the La Selva Flora Project. The site's arboretum includes more than 1300 trees of 230 species. The Station Naturalist (O. Vargas) can provide preliminary identifications for sterile material of much of the flora. Equally important, at only 1.5–2 hrs. from La Selva, the principal investigators of the "Manual to the Plants of Costa Rica"

project (B. E. Hammel and M. H. Grayum, with collaborator N. Zamora) are based at Costa Rica's National Biodiversity Institute (INBio) and have generously helped with identification of problematic taxa. Costa Rica's national herbarium (CR) also maintains a large curated collection in San José.

#### THE LA SELVA GRID

In 1991, a remarkable tool for spatially referenced field research was installed at La Selva: a reserve-wide grid system. Covering all 1550 ha of La Selva, the grid consists of permanent marker posts at 50 m  $\times$  100 m spacing, surveyed (x, y, and z) to decimeter accuracy. The 6000+ points surveyed during the installation of the grid also provided the means to generate a topographic map of the entire reserve. We know of no other tropical rainforest with anything approaching this level of baseline spatial information (the closest would be the growing world network of 50-ha tropical forest plots [Condit, 1995], which are gridded at a 5 m  $\times$  5 m spacing). Scientists working in temperate forests are likely to take for granted the availability of topographic maps such as the U.S. Geological Survey quadrangles for the United States. Virtually all tropical forest sites, however, lack such fundamental site data. For this reason, there has been very little spatial referencing and analysis of landscape composition in tropical field studies.

The grid has revolutionized how researchers design and carry out their field studies at La Selva. Now, any organism or observation can be mapped within the forest simply by measuring to the nearest grid post. Most La Selva researchers currently spatially reference their field data. This makes it possible to relate their findings to data from other projects and to baseline site information. In addition, the grid provides a basis for systematic, highly replicated sampling over large expanses of forest, a prerequisite for assessing how species vary across the landscape.

#### A RESERVE-WIDE SOILS MAP

In the early years of research at La Selva, the reserve was considered to include four broad soil types (cf. Hartshorn, 1983): "Recent Alluvium," the most fertile sites, currently episodically flooded by the major rivers; "Old Alluvium," higher areas of intermediate fertility interpreted to be river terraces from the Pleistocene; "Swamp," the permanently or seasonally wet zones within La Selva; and "Residual," the largest portion of the reserve, with broken topography and infertile soils produced by in-place weathering of the underlying lava flows.

This broad classification scheme, however, was unsupported by landscape-scale soil chemical studies or soil mapping. It is perhaps not surprising that most research at La Selva was carried out without regard to the forest's edaphic variation.

In 1987, however, this situation was radically changed when a professional soil survey was carried out. The resulting 1:10,000 soil map of La Selva (Sancho & Mata, 1987) may be the most intensive soil mapping available for any comparable area of tropical forest worldwide (P. Sollins, pers. comm.). Sancho and Mata used extensive field reconnaissance, analysis of large numbers of grab samples, and more detailed analysis of soil profiles to demarcate 23 soil consociations and 1 complex. La Selva's soils were shown to range from infertile ultisols, a dominant soil type of the world's tropics (Richter & Babbar, 1991), to relatively fertile entisols and inceptisols (Sollins et al., 1994). The advent of the soils map and considerable "consciousness-raising" of the researcher community by resident soil scientists and ecosystem ecologists have stimulated most current field researchers to factor La Selva's edaphic variation into their studies, just as they stimulated us to investigate the landscape-scale mosaics of tree community composition within the forest.

As valuable as it is, the La Selva soils map is not a static, definitive resource. It is, and should be, constantly evolving as new information comes in. Further, as found for soil maps in other parts of the world (cf. Lathrop et al., 1995; Oberthur et al., 1996), it will always incorporate uncertainties at some scales. Sancho and Mata (1987) did their soil survey before there was a grid, a topographic map, or a reliably surveyed map of the reserve; thus, there were bound to be errors in their delimitation of soil units. Second, their map depicted patterns at a scale of 1:10,000. Such a map inherently involves uncertainty at the finer scales of the phenomena studied by most field researchers. Soil map units by definition have inclusions of other soil types, and this is necessarily the case in sites like La Selva with substantial soil variation at the very local scale, a condition likely to be general within tropical soils (Richter & Babbar, 1991). Sancho and Mata's consociations are defined as mapping units within which  $\geq 75\%$  of the area is the described soil type. Finally, as in plant taxonomy, there are soil splitters and lumpers. Whether La Selva's important soil variation comprises 24 units or many fewer ones (or many more) is a matter for researcher evaluation, and the answer is likely to vary with the organism or phenomenon being studied. For our studies of tree distributions within La Selva, David



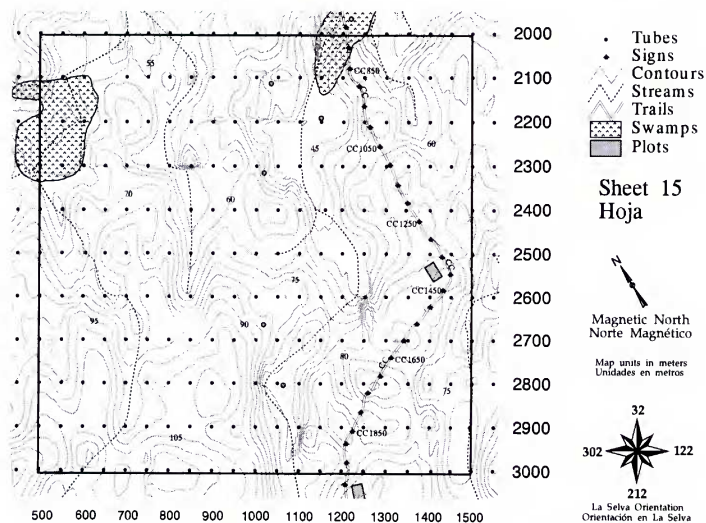


Figure 2. An example of a field map detailing GIS data for one quadrangle within La Selva (map produced by J. Juárez, OTS).

Clark and I modified the soils map both by aggregating consociations and by refining Sancho and Mata's (1987) consociation boundaries after carrying out intensive grid-based soil sampling (see below).

#### THE LA SELVA GIS

In 1989 OTS initiated a GIS for the station. The on-site GIS lab includes two Sun workstations that run the GIS software ARC/INFO, a large-format plotter, and a digitizer. Early system development involved major donations of equipment and financial support,<sup>1</sup> as well as an extensive investment of time in design and set-up by experienced GIS personnel. The station now maintains a full-time GIS manager for data updating and maintenance and to help individual system users. General-use data layers that have been incorporated into the GIS (e.g., Fig. 2) include site topography, stream and river courses, boundaries and trails, the soils map, current and past land use, locations of study plots, and the 3000+ grid posts. Remote-sensed imagery of the reserve and surrounding region is also being incorporated. Researchers are increasingly using

the grid to spatially reference their field data, incorporate them into the La Selva GIS, and then relate them to the other available data layers. For our studies of tree distributions within La Selva, the GIS was a critical resource.

#### GIS AND SYSTEMATIC SAMPLING REVEAL MOSAICS OF TREE DIVERSITY WITHIN A TROPICAL RAINFOREST

Over the last several years, David Clark and I and several collaborators have taken advantage of the research tools at La Selva to investigate how tree community composition varies within the old-growth forest landscape. We began with a study focusing on the large palms, then used the grid and GIS to assess the distributions of a core set of tree species under long-term study, and most recently have scaled up to study the spatial variation of overall tree floristics. In all three cases we have evaluated patterns at the scale of multiple 100s of hectares. This landscape-scale focus and an integration of site data with tree distributions have revealed previously unrecognized levels of internal heterogeneity within this forest.

Table 1. The seven taxa of canopy and subcanopy palms (Arecaceae, subfamily Arecoideae) in old-growth forest at La Selva. Tribes and species names from Henderson et al. (1995). Vouchers are specimens in the Costa Rican National Herbarium (CR). Summary relationships are from analyses in Clark et al. (1995).

Tribe	Species [Voucher No.]	Association between: <sup>1</sup>			
		Density (stems/ha) and soil type	Soil/ topography	Occurrence (presence/absence) and:	Harvesting
Iriarteae	<i>Iriartea deltoidea</i> Ruiz & Pav. [Chacón et al. 1968]	+	—	[local absence]	+
	<i>Socratea exorrhiza</i> (Mart.) H. Wendl. [Stevens 24559]	+	—	[everywhere]	—
Arecaceae	<i>Prestoea decurrens</i> (H. Wendl. ex Burret) H. E. Moore [Grayum & Jermy 6783]	+	+	[alluvial/flat]	—
	<i>Euterpe precatoria</i> Mart. var. <i>longevaginata</i> <sup>2</sup> (Mart.) Andrew Hend. [Grayum 7813]	+	+	[residual/slopes]	—
Geonomeae	<i>Welfia regia</i> H. Wendl. ex André <sup>3</sup> [Wiemann & Rich 137]	+	—	[everywhere]	—
Cocoeae	<i>Astrocaryum confertum</i> H. Wendl. ex Burret [de Nevers & Hammel 7820]	rare in upland			
	<i>Astrocaryum alatum</i> H. F. Loomis [Stevens 24625]	rare in upland			

<sup>1</sup> + a significant association; — no such association (from Clark et al., 1995).

<sup>2</sup> "*Euterpe macrospadix* Oersted" in Clark et al. (1995).

<sup>3</sup> "*Welfia georgii* Wendl. ex Burret" in Clark et al. (1995).

#### NON-RANDOM DISTRIBUTIONS OF THE LARGE PALMS

Palms are an important component of the La Selva old-growth forest. The seven species of subcanopy and canopy palms (Table 1, henceforth referred to by genus) comprise 25% of all woody stems  $\geq 10$  cm in diameter (Lieberman et al., 1985a). This abundant species group has significant impacts on forest structure—the large palms' dense canopies can strongly affect the distribution of light environments in the understory, and the senescing and falling of their massive leaves contributes to the high levels of physical damage to smaller plants below them (cf. Vandermeer, 1977; Clark & Clark, 1989). The fruits of several of these palm species are also important in the diets of diverse mammal species (Levey et al., 1994; Timm, 1994). For all these reasons, it is of interest to know how this guild of plants is distributed within La Selva. Does the group as a whole vary in density among different sectors of the landscape? Do any of the component species show non-uniform distributions within the old-growth forest?

Approaches to such questions about tropical forest composition have usually involved evaluating plant species abundances within one to a few plots or transects selected by the researcher as representative of the forest as a whole (a notable exception is the pioneering work of Ashton [1964, 1969] and Austin et al. [1972]). Such a design has been to a large degree mandated by both the lack of base maps of site variation and the difficult logistics within such forests. Although enumerating all species within a plot is indeed the only way to study numerous aspects of plant population structure and dynamics (cf. Dallmeier, 1992), this approach is not suited for generalization to the larger landscape, and the findings can be uninterpretable in terms of specific site variables, such as topography or soil type. One illustration of these issues is given by data from three upland forest inventory plots within La Selva (Hartshorn, 1983), which provided striking evidence of non-uniform distributions of the large palms. In all three plots (2, 4, and 4 ha), the second most abundant tree species  $\geq 10$  cm in

diameter was a palm, but the species was different in each plot (*Iriartea* in Plot IIb [Alluvial Soil]; *Welfia* in Plot I [Alluvial Soil plus some Swamp; and *Iriartea* was absent from this plot; Hartshorn & Hammel, 1994]; *Socratea* in Plot III [Residual Soil]; species names of the single representative of each genus at La Selva are given in Table 1). Although these plot data demonstrate that the distribution of large palms varies markedly within La Selva, they are insufficient for assessing how these distributions relate to the forest's soil and topographic variation.

The advent of GIS and the grid at La Selva, however, made possible a radically different approach to assessing plant distributions within the old growth. The grid, with its 50 m  $\times$  100 m spacing, was a set of precisely located points spread over the entire forest. Using them as sample points, we could systematically sample a large landscape. By assessing palm distributions this way in many watersheds and terrain types, and in different forest stages (gap to mature forest) and topographies within each soil type, we could achieve a level of environmental replication difficult to achieve with other methods.

To investigate the landscape distributions of large palms at La Selva, we selected a 568-ha sector of the upland (non-swamp) old-growth forest. We then assessed the presence/absence and local abundance of the seven species at each of 516 grid intersections within this study area. We used our field notes regarding streams, swamps, and topography to refine the Sancho and Mata (1987) soils map, and we used the GIS to aggregate soil associations into four contrasting units: Alluvium (most fertile, with gentle topography); Streams (the valley soils of the principal streams); Residual soils (broken terrain, soils weathered from lava); and Arboleda (a problematic area of steep topography, thought to be of intermediate fertility [Sollins et al., 1994]). In the field we also classified each sample point in terms of topographic position. The methods, results, and statistical analyses of this study are detailed by Clark et al. (1995). Here I highlight several findings that demonstrated a spatial substructuring of this forest previously invisible to us and dozens of others who have worked at the site for a decade or more.

We found that the total abundance of the canopy and subcanopy palms varies greatly across the landscape. Larger individuals of this guild (stems  $\geq 10$  m tall, all species combined) continuously decrease in density from slope crests, to slopes of decreasing steepness, to slope bases and flat terrain. Over this topographic gradient the density of

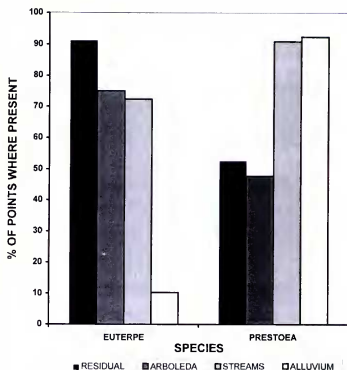


Figure 3. Contrasting soil affinities of *Euterpe precatoria* and *Prestoea decurrens* (from Clark et al., 1985). Data for each species are the percent of the sample points in each soil type at which any individual  $> 1$  m tall was observed. Sample points per soil type (soil descriptions given in text): Residual, 329; Arboleda, 44; Streams, 65; Alluvium, 78. For both species the association between presence/absence patterns and soil type was highly significant ( $\chi^2$ ,  $df = 3$ ,  $P < 0.0001$ ).

large canopy and subcanopy palms declines by a factor of two. Such spatial heterogeneity in the abundance of these palms within La Selva must have widespread impacts on forest structure and on processes as diverse as mammal activity and understory light environments.

The species-level distributions of these palms revealed further evidence of substructuring within the forest. All five of the species that were not rare in upland forest showed highly significant variation in local density or overall presence/absence patterns with respect to the spatial variation in topography and soils within La Selva (Table 1). One closely related species pair, La Selva's single species of *Prestoea* and single species of *Euterpe* (Table 1), showed strong but contrasting edaphic associations, both with soil type (Fig. 3) and with topographic position. *Euterpe* was strongly biased toward steep topography and the less fertile soils. *Prestoea*, in contrast, while nearly omnipresent on gentle topography, was absent at half the sample points on the soils with steep slopes. The most abundant large palm, the single *Welfia* species (Table 1), strongly varied in density across the four soil units although it was present everywhere (at 100% of the sample points).

The use of GIS to investigate the spatial distri-

butions of these large palms revealed yet another striking feature of the La Selva old-growth forest that was previously unsuspected. From one sector of what had often been considered "virgin forest," the otherwise omnipresent canopy palm *Iriartea deltoidea*; Table 1) is nearly completely absent. The most probable explanation for this anomalous distribution is local removal by historic human harvesting. Our analyses demonstrated that the patterns of presence/absence for both *Iriartea* and the closely related *Socratea* (*exorrhiza*; Table 1) were insensitive to both soil type and topographic position. *Socratea* was omnipresent within the old-growth forest. Similarly, *Iriartea* was omnipresent on all soil types, except in one zone of Alluvium close to former human habitation and easy river access. By interviewing local residents we found that *Iriartea* was the most sought-after native palm taxon for its large and tasty meristem ("heart-of-palm") and its robust, durable stems, which were used in construction. That *Socratea* remained in this sector of the forest is probably due both to the bitter taste of its meristem ("palmito amargo") and to its more slender stems, less useful for building. This evidence of prior human impact on tree floristics within this intensively studied sector of the La Selva old growth has changed how the forest is viewed. In addition to being key background information for many of the studies carried out in this particular sector, this finding has stimulated La Selva researchers to be on the alert for evidence of other human impacts within the old growth.

#### GIS REVEALS EDAPHIC ASSOCIATIONS OF CANOPY AND EMERGENT TREES UNDER LONG-TERM STUDY

When the grid and GIS were installed at La Selva, they offered an opportunity to investigate the spatial distributions of the tree species David Clark and I had under long-term demographic study in the old-growth forest. Since 1982 we have accumulated samples of individuals of all post-seedling life history stages (from 50-cm-tall saplings to adults) of nine ecologically contrasting species of canopy and emergent trees at La Selva (voucher numbers are for specimens deposited in the Herbario Nacional de Costa Rica): *Dipteryx panamensis* (Pittier) Record & Mell (Papilionaceae) [R. Robles 1199]; *Minquartia guianensis* Aubl. (Olacaceae) [G. Herrera 2250]; *Lecythis ampla* Miers (Lecythidaceae) [R. Robles 2208]; *Hymenolobium mesoamericanum* H. C. Lima (Papilionaceae) [R. Aguilar 19]; *Pithecellobium elegans* Ducke (Mimosaceae) [B. Hammel 17319]; *Hyeronima alchorneoides* Allemão (Euphorbiaceae) [Chacón 751]; *Simarouba amara*

Aubl. (Simaroubaceae) [R. Robles 1670]; *Cecropia insignis* Liebm. (Cecropiaceae) [W. Burger 11135]; and *Cecropia obtusifolia* Bertol. (Cecropiaceae) [R. Robles 1446]. Our annual measurements of survival, growth, and microsite of > 2800 individuals have enabled us to evaluate these species' ontogenetic growth patterns, relation to light environments and forest dynamics, and sensitivity to yearly climatic variation (cf. Clark & Clark, 1992, 1994; Clark et al., 1993). Before the advent of the GIS and the grid, however, our understanding of these trees' relation to the edaphic variation within La Selva was limited to an intuitive sense that *Dipteryx* was associated with the Alluvium and *Pithecellobium* with the Residual soils. We have recently used the new spatial tools at La Selva to refine our understanding of edaphic variation within the forest and then to assess the distributions of our nine focal tree species with respect to this variation (D. B. Clark et al., 1998).

To refine the soils map, we used the grid intersections as a framework for systematically sampling the soils within a 573-ha section of the reserve (one soil sample from 50-cm depth at each of 1171 grid points). We arrayed the resulting soil samples geographically and then classified each into a soil type, following the concepts originally developed by Sanchez and Mata (1987) and Sollins et al. (1994). For classification, we combined soil color with our field-collected data on each point's topographic position and slope angle and with GIS data for point elevation and surrounding terrain (from a kriged digital elevation model of La Selva based on the 6000+ surveyed points). We delimited polygons following elevational contour lines around the spatial groupings of soil units at grid points, and then digitized the resulting soils map into the La Selva GIS. Although our analysis largely confirmed the previous soil mapping of the reserve, it did result in some significant changes in unit boundaries and a more intuitive geographic relation between site geomorphology (Alvarado I., 1990) and the soils. It also significantly altered our understanding of soil variation in some areas that had been study sites for diverse research studies within La Selva (see below). For our study of the edaphic associations of the nine tree species, we aggregated the upland soil types into three broad units: Old Alluvium (excludes the currently floodable Recent Alluvium), Residual, and Stream Valley.

We had previously mapped our tree population samples into the GIS by referring each tree in the field to the grid (by measuring distance and compass bearing to the nearest grid post or to the nearest tree that had been so mapped), and then incor-

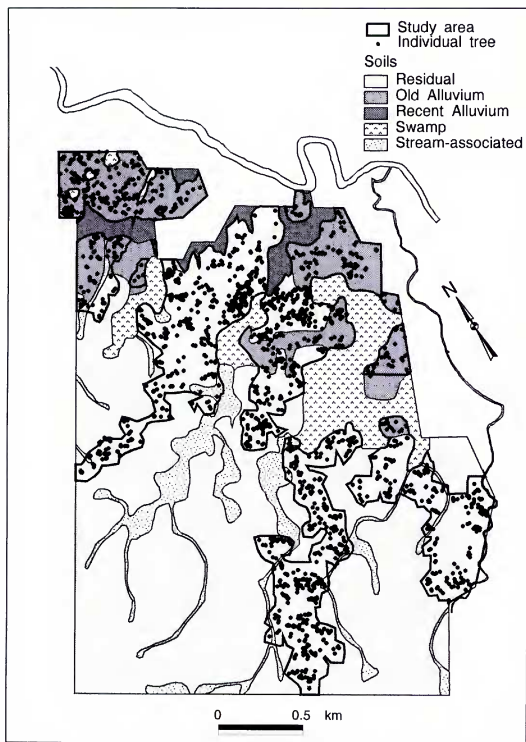


Figure 4. A GIS-generated map of the 216 ha area (demarcated by thick black border) encompassing the long-term study populations of our nine focal species of canopy and emergent trees at the La Selva Biological Station, Costa Rica. Individual trees are indicated by black dots. The underlying soil map (described in the text) is a refined version of the original (Sancho & Mata, 1987) La Selva map.

porating these tree location data into the GIS. Although this process was very time consuming (more than 1 person-year of work), it created a permanent spatially explicit data set for the long-term population ecology studies, and it was a prerequisite for a tree  $\times$  soil analysis. For this analysis, we used the GIS to delimit the old-growth areas of La Selva containing our tree samples, overlaid this map on the new soils coverage (Fig. 4), and then used the included grid intersections to generate the expected (background) distributions of both soil and topography within our 216-ha study area.

This GIS analysis revealed that, in the upland old-growth forest, all nine of our study species had non-random distributions associated with one or more features of La Selva's edaphic variation. Most of the highly significant associations ( $P < 0.005$ ) were with soil type (6 species). Within their preferred soil, three of the nine species also showed highly significant biases with respect to topographic position. As we had suspected, the distribution of *Pithecellobium elegans* was strongly skewed toward the Residual soils, and that of *Dipteryx panamensis* was biased toward the Alluvium. Both species, however, showed



additional biases that we had not perceived during many years of fieldwork: *P. elegans* was preferentially on flat ridgetops and biased away from slope bases within the Residual soils, while the distribution of *D. panamensis* within the Alluvium was biased toward gentle slopes and away from flat terrain. Another discovery was that La Selva's two *Cecropia* species had strong, contrasting edaphic associations (*C. insignis*: Stream Valley soils, lower slope angles; *C. obtusifolia*, higher slope positions, but no bias regarding slope angle or soil type).

#### SCALING UP: THE EDAPHIC ASSOCIATIONS OF THE LA SELVA TREE FLORA

We have recently scaled up these approaches to analyze distribution patterns within the total La Selva tree community and their relation to soil type and topography. We once again have used the grid as a basis for systematic, highly replicated sampling of old-growth forest, this time including the swamps. At each grid intersection ( $N = 1171$ ) in 573 ha of La Selva old growth, we established a 0.01-ha circular plot within which we measured and identified all tree stems of  $\geq 10$  cm diameter (5127 stems total).

This landscape-scale approach has provided new insights about how tree diversity is distributed within La Selva. The sample, which includes 253 of the 323 tree species known from La Selva, also resulted in the addition of 15 new species to the site's tree list. One of these, *Caryodendron angustifolium* Standl. (Euphorbiaceae), represents a genus new to Costa Rica. These finds are a result of the process of "ecological collecting," the challenging work of identifying all trees in a plot, including the non-reproductives. This approach to tropical forests is very different from that taken by taxonomic specialists, who naturally focus on the plants that are flowering or fruiting when they visit a site (Gentry, 1994). As Gentry pointed out, even some of the more common species found in an all-stem inventory in a given tropical forest can turn out to be new to the site or to science. Additionally, our sampling over the whole landscape turned up numerous examples from the "tail of the species distribution" (B. E. Hammel, pers. comm.)—those many tree taxa that are locally very rare within any tropical rainforest. Such discoveries improve understanding both of local site biodiversity and of species distributions at larger spatial scales within tropical forest regions.

In addition to these new finds, use of the GIS for spatial examination of the data set (D. B. Clark et al., unpublished data) has revealed extensive substructuring of the tree community across this rainforest

landscape (Fig. 5). As with the guild of large palms, some other tree species are strongly associated with certain soils (e.g., Fig. 5A, *Castilla elastica* Sessé in the Old Alluvium and Recent Alluvium). Additional interesting distribution patterns are evident for many tree species. For example, *Lonchocarpus oliganthus* F. J. Herm. (Fig. 5B) is associated with the Recent Alluvium, the Swamp soils, and with the Stream Valley soils that meander through the Residual Soil region of La Selva. These soil units range from nutrient-rich (Recent Alluvium) to strongly infertile (Stream Valley soils); this species is able to grow over a wide range of soil fertility but only in sites that are wet or floodable. Another distribution pattern found for numerous species is that shown by one of the canopy-level *Matisia* species (Bombacaceae) at La Selva, *M. ochroleuca* K. Schum.; although confined to the Residual soils in La Selva, this species occupies only a restricted area within this soil type (Fig. 5A). With this type of distribution, factors other than the variation among major soil units must be playing a role. One possibility is individualistic responses of tree species to combinations of particular soil characteristics, such as certain cations, P, N, pH, soil organic matter, or texture, coupled with substantial variation in these characteristics within soil units. Such complex idiosyncratic edaphic associations were found to characterize many tree species in tropical rainforest areas of Sarawak, Borneo (Baillie et al., 1987). To investigate this possibility, our next step will be to go beyond the "typic" characterization of soil variation so far used at La Selva and to measure and map individual soil properties across the landscape. We will analyze a large suite of soil characters from each of the sample points used in this study and then combine GIS and multivariate techniques to examine them for associations with the non-random distributions of trees within La Selva. This factor-level approach will greatly aid interpretation of the currently enigmatic distributions of many of the species.

In addition to revealing the mosaic nature of the tree community in this tropical rainforest, this GIS-based analysis has also produced new evidence suggestive of past human activity deep within the old-growth forest. Within one of our 0.01-ha tree inventory plots in well developed forest in La Selva's center, 80 m from the nearest trail and more than 1 km from any historic human habitation (Fig. 5a), we found a tree of the species of cultivated avocado, *Persea americana* Mill. (Lauraceae). This species has been found in very old archaeological deposits (7000 B.C.) in the Americas (Simpson & Connor Ogorzaly, 1986). The site where we encountered this tree is very close to where charcoal was found within the soil profile by researchers (R.

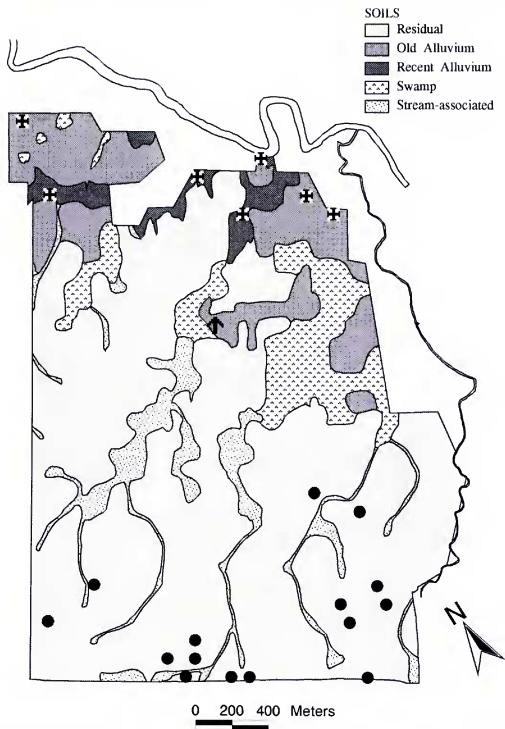


Figure 5. Examples of spatial substructuring of the tree community in upland old-growth forest at La Selva. Symbols indicate the occurrences of a given species in the 0.01-ha plots centered on all grid intersections ( $N = 1171$ ) within this 573-ha sector of forest. The soil map is as in Figure 4. —A (this page). Three species' distributions in the sample plots: crosses, *Castilla elastica* (Moraceae); arrow, *Persa americana* (Lauraceae); dots, *Matisia ochroleuca* (Bombaceae). —B (next page). Occurrences of *Lonchocarpus oliganthus* (Papilionaceae) in the sample plots (crosses).

Sanford, Jr. & S. Horn) investigating the reserve's history (Horn & Sanford, 1992, and unpublished). By the original soils map (Sancho & Mata, 1987), the site plots out within the infertile Residual soils that cover most of La Selva, a puzzling location for the kinds of indigenous human activity suggested by the tree and charcoal. However, when we overlaid this collection point on our refined soils map (based on grid-based soil collections, see above), we found this site to be within a previously unrecognized zone of (more fertile) Old Alluvium within the Residual soil region. This is a classic case of

how such GIS data syntheses can enhance the results of individual studies. Taken by themselves, these lines of evidence are much less interesting than when combined through spatial referencing.

#### SCALES OF SPATIAL VARIATION WITHIN TROPICAL RAINFORESTS, AND THE TOOLS TO INVESTIGATE THEM

##### DIFFERENT LEVELS OF WITHIN-FOREST EDAPHIC MOSAICS

It is becoming increasingly clear that marked internal heterogeneity is an important characteristic of

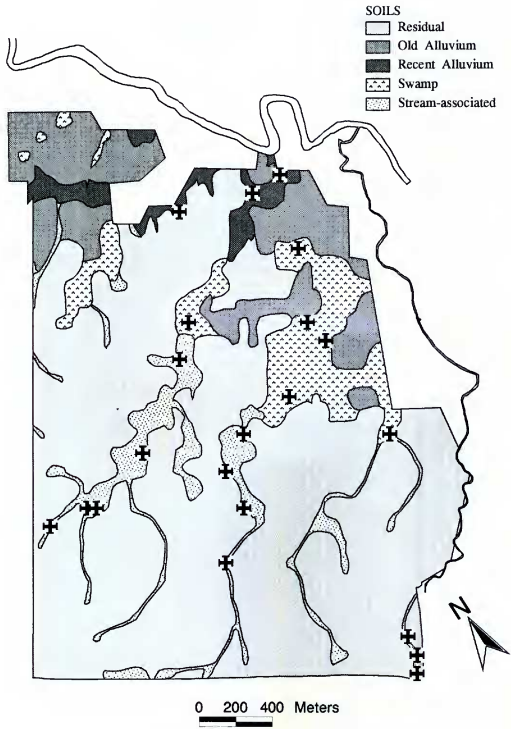


Figure 5. Continued.

the tropical rainforest biome (Ashton, 1964; Austin et al., 1972; Baillie et al., 1987; Kahn, 1987; Gentry & Ortiz S., 1993; Ruokolainen & Tuomisto, 1993; Tuomisto et al., 1995; Clark et al., 1995; Duivenvoorden, 1996; Clark, present study). Recognizing and interpreting the spatial mosaics within these forests will be fundamental to both understanding and conserving their great biodiversity. The markedly different scales of important spatial variation, however, will require distinct research approaches.

At one scale are structurally distinct forest types that can be distinguished by field reconnaissance, visual inspection from small planes, or interpretation of remote-sensed data. Examples of visually distinct patches that harbor particular floras are

swamp forests dominated by a few species of large palms and the stands of low canopy and small-diameter trees found on very infertile white sands across Amazonia. Assessing how such strongly contrasting patches are distributed within tropical rainforest landscapes is a vital need for understanding the spatial distribution of biodiversity within the biome (cf. Tuomisto et al., 1995). Evaluation of the community-level biotic differences among these patch types is also needed. Given the dramatic vegetation shifts between these readily distinguishable forest types (cf. Tuomisto et al., 1995; Duivenvoorden, 1996; Terborgh et al., 1996), inventorying a few plots or transects within each should adequately indicate major distinctions among them.

A second level of tropical forest mosaics is of those occurring *within* one of these patch types and thus across much more limited gradients of environmental variation. This is the scale that we have been principally investigating within La Selva: the internal heterogeneity of an upland tropical forest landscape, in the absence of extreme intra-site contrasts such as those occurring on adjacent terraces within floodplains or where white sand and clay-dominated soils are interdigitated (cf. Duivenvoorden, 1996). As we have shown, even at this "within-patch" scale, the tree community composition of tropical moist forest can show marked spatial variation. We found much of the internal heterogeneity in the La Selva tree flora to be associated with local variation in soil types and topography, even though the total relief and the total range of soil characters were quite constrained subsets of those found more regionally in the lowland wet tropics. Most of these tree-site associations, even some of the most striking ones, were previously unrecognized, despite the long history of research at this site.

For our investigation at La Selva of this more local scale of internal variation within tropical rainforest, the combined use of landscape-scale systematic sampling and GIS proved to be critical. By spreading out the sampling over 100s of hectares of forest, we obtained highly replicated, spatially separated observations of tree floristics within each major soil unit and in each type of topographic situation (positions along the ridgetop-to-swale catena and different slope angles). Had we assessed these factors within a single plot or transect, even a very large one, we could not have generalized our findings to the larger landscape due to the possibility of sample bias from particular local edaphic or historic conditions. The 50 to 100 m intervals between neighboring sampling points also reduced the likelihood of spatial autocorrelation among samples (cf. Clark et al., 1996). Finally, the GIS enabled us to relate several classes of complementary site information to the patterns we discovered in the tree distributions. A particular additional strength brought by GIS to such work is that it provides an ongoing link to the site database, even as it is being expanded and refined through time. This combined research approach thus seems well suited to both assessing and interpreting the landscape-scale spatial variation in floristics within a given type of tropical rainforest. A further analytical step that could significantly enhance the data interpretation would be to use generalized linear modeling (GLM) to evaluate the simultaneous (combined) effect of multiple site factors (e.g., soil type, topography, and

disturbance history) on the tree species' distribution patterns (cf. Austin et al., 1996).

#### RECOGNIZING HUMAN "FOOTPRINTS"

In addition to edaphic variation, past human interventions, from silviculture to swidden agriculture to selective cutting, are an important potential source of within-landscape heterogeneity in tropical rainforest. This is true even in stands considered old growth, as we found at La Selva. Indeed, an accumulating body of research findings indicates that most tropical forests are likely to have been affected this way (e.g., Gordon, 1982; Anderson, 1990; Gómez-Pompa & Kaus, 1990; Brown et al., 1991; Bush & Colinvaux, 1994; Garcia-Montiel & Scatena, 1994). Given the likely pervasiveness of such impacts, researchers studying the distribution of biodiversity within these forests should explicitly seek indications of human activities in their study sites (Hamburg & Sanford, 1986). As we found at La Selva, evidence of such anthropogenic impacts can emerge when landscape-scale floristic patterns are assessed for non-random distributions beyond those attributable to the site's edaphic variation. For this kind of question, the combined use of GIS, edaphic surveys, and systematic replicated vegetation sampling seems a useful approach.

#### CAN IT BE DONE ELSEWHERE?

Is this La Selva experience translatable to other, less developed sites in the tropics? One newly available research tool makes the answer to this increasingly yes. The Global Positioning System (GPS) is a technology for field determination of locations by interpretation of satellite signals. A field researcher in any tropical forest can now use a portable GPS receiver with extendable antenna, run in parallel with a GPS station at their base site, to measure field locations with good to excellent accuracy (recent trials under canopy in a suite of U.S. forests produced accuracies of ca. 2–8 m; Deckert & Bolstad, 1996). This technology will also rapidly become both less expensive and more effective (the U.S. administration recently resolved to remove the current system of signal degradation, probably within 10 years). Although using GPS requires significant training and equipment, the benefits are immense for field researchers.

Now, any tree or vegetation type encountered in the most remote tropical forests can be spatially referenced so as to be relocatable by anyone. Thus "ecological collecting," the inventorying and identification of even non-reproductive plants, becomes feasible anywhere, because sterile plants can be

precisely mapped for repeated visits until found fruiting or flowering. Well documented location data made generally available to the research community will maximize the current and future value of the very limited systematic and ecological work within these forests. We should begin to think of the entire tropical forest biome as a "permanent study plot."

This new tool also makes feasible in any tropical rainforest the type of landscape-scale/GIS research we used at La Selva. With GPS any field researcher can carry out highly replicated, systematic sampling over 100s of hectares, without depending on a very expensive physical grid such as La Selva's. When site variables as well as vegetation are assessed at all sample points, the ground is laid for a synthetic GIS analysis of the relation between floristic patterns and site conditions at the landscape scale. None of these elements, however, are easy to attain. Those starting from ground zero in a tropical forest site will find that considerable effort is involved in achieving each component of such an approach: the use of GPS in the field; the determination of site factors, particularly soil characteristics; plant identification; and the analysis of the resulting data with GIS. Our strongest recommendation based on our experiences at La Selva is to build multidisciplinary research teams incorporating expertise in all these fields, rather than having individual researchers trying to develop all the necessary skills. Such a team brings in the needed levels of prior training and experience in these new areas, and thus ensures the quality of data produced.

## CONCLUSIONS

The biodiversity of the world's tropical rainforests is still largely unstudied and unprotected. These are compelling reasons for increasing current research efforts to understand the geographic and local variation of the biota within these ecosystems. Recent studies in different parts of the tropics have demonstrated a high level of within-forest mosaicism. This is an important new dimension of complexity that must be understood if current conservation efforts in this biome are to be effective. As shown by our research experiences in one Central American forest site, the combined use of GIS and highly replicated systematic sampling of site and biotic variables over meso-scale landscapes (100–10,000 ha) is one promising strategy for deepening current understanding of the great spatial variation within the world's tropical rainforests.

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